

The Organization of Gaze Control in the Blowfly *Calliphora erythrocephala*

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Abstract - Flies have a distinct body posture during walking and flight. Hence head and eyes have mostly a preferred alignment with the surroundings. Voluntary and involuntary changes of body orientation elicit compensatory head turns which stabilize the original, correct orientation of the eyes relative to the surroundings. Compensatory head turns are elicited by several sensory cues which simultaneously influence the fly's walking posture or flight attitude, depending upon the locomotor state. Head/trunk-coordination is achieved by directionally specific neck sense organs. Visual and mechanosensory response components have complementary kinetic and dynamic characteristics. This enables the fly to correct unwanted misalignments of its eyes rapidly and precisely over a large range of angular velocities. The fly thus optimizes its visual abilities despite its formidable maneuverability.

Introduction

Flies have, like other animals, a preferred body posture. When walking, it is determined by the contact with the ground: the body axis is roughly horizontal, and the back is directed upwards. The flight attitude is similar but the body axis may be more elevated, especially in slow flight (Wagner 1985, David 1985). Very probably, the fly's sense organs and sensory nervous system have been adapted, during evolution, to work best in this preferred orientation.

Flying insects may turn around the vertical (yaw) without affecting flight equilibrium. Any rotation about a horizontal axis (transverse axis: pitch turns; longitudinal axis: roll turns) bears, however, the risk to crash unless flight balance is quickly stabilized by equilibrium reflexes (Schöne 1980, Hengstenberg et al. 1986).

The tasks of good vision and equilibrium control may require different alignments with the surroundings: during fast and narrow turns, for example, the fly has to bank sideways to account for the centrifugal acceleration (Hengstenberg et al. 1986). The optical surround, on the other hand, retains its usual orientation. Therefore it may be advisable to keep the eyes aligned with the vertical i.e. to counter-roll the head during banked turns.

Insects have two kinds of eyes: (1) the three dorsal ocelli are small camera eyes, with a single underfocussed wide-angle lens, which are best suited to sense global brightness in the dorsal hemisphere. (2) the two large compound eyes, consisting of several thousand mosaic eyes (ommatidia) which resolve spatial details in the lateral hemispheres of visual space. Both kinds of eyes are part of the head capsule and can therefore only be moved by turning the head.

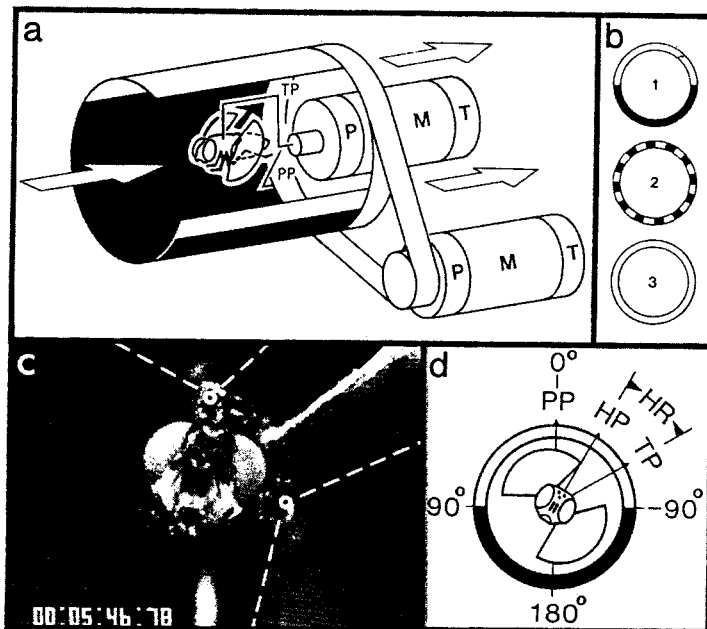


Figure 1:

(a) Wind-tunnel to elicit and observe head movements in the blowfly during stationary flight. Servomotors (M), fitted with position (P) and speed-sensors (T) allow to roll independently the fly and its optical surroundings. Angular positions are indicated in the video records by pointers (TP, PP). Wind flowing through the tunnel (arrows, 2 m/s) increases the flight mood of flies. (b) Cross sections of patterns lining the tunnel. (c) Videoframe as recorded through the entrance nozzle. Note that the fly generates simultaneously a compensatory head turn and a corrective difference in wingbeat amplitudes when tilted to its left. (d) Measures and sign conventions; HR [°] = head roll angle, referred to the fly's trunk.

The blowfly *Calliphora erythrocephala* can turn its head about all three principal axes (yaw and pitch $\pm 20^\circ$, roll $\pm 90^\circ$; Hengstenberg et al. 1986). The mechanics of the neck joint, the structure and insertions of the neck muscles, and their motoneurons have been studied in detail (Strausfeld et al. 1987). Physiological properties of motoneurons are partly known by electrophysiological investigations (Milde et al. 1987). Head movements of insects are very difficult to observe in free flight (Wagner 1985, Zeil 1983). Voluntary stabilizing movements of the head could, however, be demonstrated in tethered flight (Land 1975, Hengstenberg 1992). Head movements in response to unexpected perturbations of the correct flight attitude can be studied during stationary flight in a wind-tunnel (Hengstenberg et al. 1986).

This article demonstrates gaze-stabilizing head movements made by the fly *Calliphora* in response to roll stimuli i.e. apparent rotations about the fly's body axis.

Methods

Flies were fixed coaxially to the shaft of a servomotor that allowed to tilt or turn them during stationary flight about the body axis (Fig 1a). The animals were surrounded by a translucent cylinder that could be lined with various patterns (Fig 1b), illuminated diffusely from the outside, and turned by a second servomotor. Air was flowing past the fly, due to a suction ventilator, at a comfortable travelling speed of 2 m/s. Head movements of the fly were observed by a small video telescope through the entrance nozzle of the windtunnel (Fig 1 c), and measured by single frame analysis. The angle between the sagittal planes of the head and that of the fly's trunk is the head roll angle ($HR [^\circ] = HP-TP$; Fig 1d).

If a fly is rolled sinusoidally during flight (Fig 2a; 1 Hz, $\pm 90^\circ$) in an environment simulating "sky" and "ground" in their normal orientation, it generates phase-locked head movements of opposite sign (Fig 2b). They reduce the overall rotation of the head, relative to the surroundings by about 2/3, and thus tend to stabilize the orientation of the eyes. At the same time the fly generates compensatory steering maneuvers by changing wing pitch and wingbeat amplitude differentially on the left and right (Fig 1c). Hence, in free flight the actual stabilization of the eyes would be even better than suggested by the head movements alone. The experiment above does not indicate whether the fly senses its own motion, irrespective of the optical surround, or whether it makes use of the relative motion between its eyes and the surroundings. Two complementary experiments show that flies use both sources of information: For the result of Fig 2c the fly was held stationary and the surround was rolled sinusoidally; the synphasic head movements prove that the fly uses visual cues to control head turn. For the reciprocal experiment (Fig 2d) the sky-and-ground pattern was removed, and the fly had to fly in optically featureless surroundings. Nevertheless, when the fly was rolled sinusoidally, it generated antiphase head movements, proving that it also senses rotations of its body independent of visual cues i.e. through a mechanosensory organ.

The visual and mechanosensory roll responses can be further decomposed by specific modification of the stimuli, combined with surgical manipulations of various sense organs (Hengstenberg 1992, 1988).

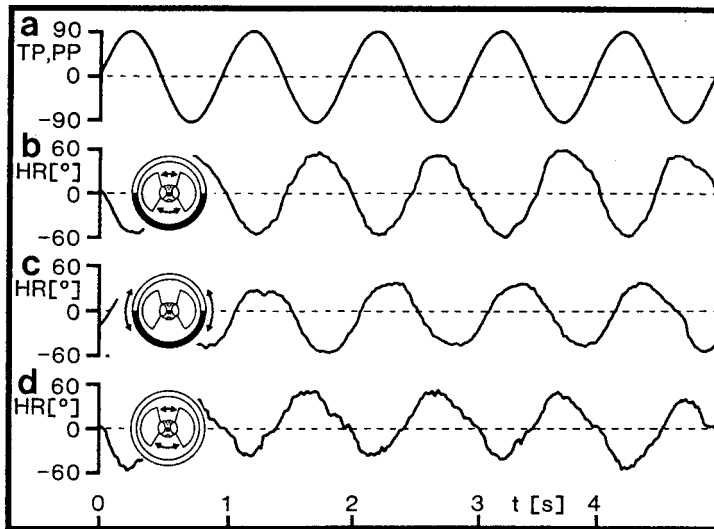


Figure 2:

Compensatory head roll of *Calliphora* in tethered flight. (a) Sinusoidal roll stimulus (1 Hz, $\pm 90^\circ$). (b) Rolling the fly inside the stationary sky-and-ground pattern elicits an antiphasic head roll compensating about 2/3 of the imposed misalignment. (c) Rolling, instead, the pattern while holding the fly stationary elicits a synphasic head turn, due to visual roll perception, which reduces the apparent misalignment. (d) Rolling the fly in optically homogeneous surroundings elicits stabilizing head turns due to body motion perception.

Figure 3 gives an overview of the response components that could be isolated so far, and are now amenable to detailed anatomical and physiological investigations. Each component is specified by its name, the mediating sense organ, and a pictogram illustrating the stimulus used for its characterization.

The *pattern motion response* (Fig 3a) is elicited by coherent roll motion of extended patterns, irrespective of the kind of pattern, as long as it can be resolved by the compound eyes. Visual motion is detected by thousands of elementary motion detectors simultaneously, where each has a very small receptive field, at a distinct location in visual space, and a specific preferred direction (Reichardt 1987, Götz et al. 1979). Widefield motion sensitive neurons in the third visual neuropil of the fly integrate spatially a selected fraction of local motion signals (Hausen 1984). Thereby signals are generated that can be used for specific control of head posture and locomotor behaviour (Hengstenberg et al., this volume). The *contour orientation response* (Fig 3b) is due to horizontal contrast edges in the frontal part of the visual field and mediated through the compound eyes.

The dorsal light response (Fig 3c, d) has two components of unequal strength: the *tonic dorsal light response* (Fig 3c) is elicited by a difference in mean brightness in the visual fields of the two compound eyes. This response is especially important for the fly because it is the only cue indicating the absolute orientation in space. The *phasic dorsal light response* (Fig 3d) is mediated by transient illumination differences of the two lateral ocelli. Compared to other insects (Stange et al. 1979, Taylor 1981) this response is very small in flies.

Among the mechanosensory roll responses, the *self-motion response* (Fig 3e) is most prominent. It is mediated by the "halteres". They are homologous with the hindwings of other insects and have been transformed, in Diptera, into "gyroscopic" sense organs for rotations (Pringle 1948, Nalbach 1993). A haltere looks like a tiny pendulum of 1 mm length: It consists of a distal knob that comprises most of haltere mass, a thin stiff stalk, and a basal swelling that is attached to the side of the fly's trunk by a hinge joint. In flight, the halteres oscillate at wingbeat frequency, but in antiphase with the wing, in a vertical plane, tilted 30° backwards from the fly's transverse plane (Pringle 1948, Hengstenberg 1988). Rotations of the fly generate periodic coriolis forces that depend upon the direction and speed of rotation, and act upon the haltere's center of mass, i.e. the haltere knob (Nalbach 1993). The strain, caused by these periodic forces, is sensed by ca. 450 highly specialized cuticular mechanoreceptors that are located in the basal swelling and organized in seven distinct fields (Pflugstaedt 1912, Gnatzy et al. 1987, Hengstenberg 1988). The projections of haltere receptors in the central nervous System are at present only coarsely known (Strausfeld and Seyan 1985, Hengstenberg et al. 1988).

Properties and processing of the receptor signals are now studied electrophysiologically (Nalbach pers. comm.). A *difference in wing-load* (Fig 3f) that may occur during righting of the body after banking, is sensed probably by cuticular strain receptors at the wing base and elicits a transient righting response of the head.

The *direction of gravity* (Fig 3g) is sensed by leg proprioceptors through the distribution of weight among the legs when the fly is walking. Depending upon substrate

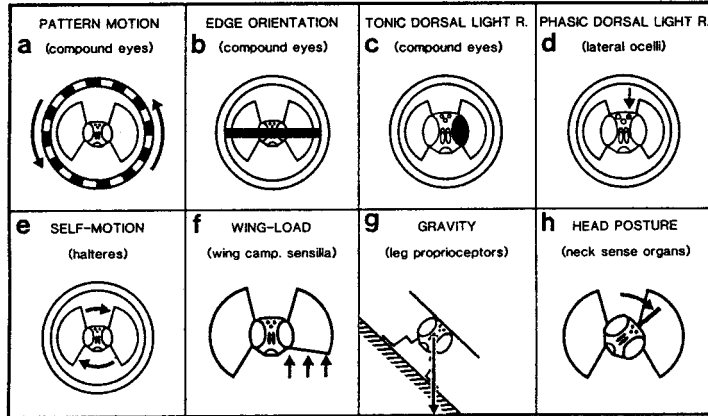


Figure 3:

Cues and sense organs for roll perception in *Calliphora*. Four separate visual (a-d) and four mechanosensory (e-h) response components can be distinguished by application of specific stimuli and elimination of particular sense organs. Gravity (g) is effective only in the walking fly. Most cues also influence the flight torque and walking posture.

inclination flies turn their head about the transverse and longitudinal axis towards an upright position (Horn et al. 1978). Since flies have no specific graviceptors, their sense of gravity is switched off automatically when they start flying. Consequently no responses to direction of gravity can be observed in flight (Hengstenberg 1988). Paradoxically, as it may seem, this is a patent means to prevent possible confusions that any kind of graviceptor would suffer from the oblique and varying linear accelerations generated along the aerobatic flight trajectories that are typical for flies.

Finally, head posture (Fig 3h) depends also on the orientation of the head. Direction-specific neck sense organs control head posture in a feedback configuration (Horn et al. 1978, Preuss and Hengstenberg 1992) and flight steering in a feed forward configuration (Liske 1977). There are two kinds of sense Organs: the prosternal organs are external mechanoreceptive hair fields which sense pitch- and roll-turns of the head (Preuss and Hengstenberg 1992), and internal chordotonal organs whose role is not yet clear.

Most of the signals that affect head posture are also used by the fly to control walking posture (Hengstenberg unpublished) and flight steering (Gaffron 1934, Götz et al. 1979, Nalbach et al. 1994, Srinivasan et al. 1977). In each of these locomotor states head- and body-turns are performed simultaneously (see Fig 1c)1. Therefore the respective angles and angular velocities have to be added if the efficiency of gaze realignment is to be judged in an unrestrained fly. Figure 4 shows a signal flow diagram summarizing the results reported above: there are two optical and three mechanical cues, transduced by six kinds of sense organs that feed into neural circuits which extract roll-specific signals. These are, in turn, distributed to motor control circuits which coordinate the activity of neck-, leg-, and steering muscles. Compensatory movements reduce the roll-error-signals physically. Switches are opened by different locomotor states (F = flight, W = walking, S = standing) and disable inputs from mechanoreceptive sense organs and inappropriate outputs.

From these findings it emerges that the orientation control system of *Calliphora* is a highly developed network for simultaneous processing of many sensory signals. Its configuration changes with locomotor states, but little is known of how these changes are brought about. Why should *Calliphora* use that many visual and mechanosensory mechanisms to stabilize its head? Signals from a single sensory System may depend upon the instantaneous orientation and motion of the fly and, in case of the visual system, also on the particular structure and lighting of the surroundings. Signals may, therefore, be not precise enough for optimal correction of attitude and course. Simultaneous use of independent signal sources is likely to increase the axis-fidelity and accuracy of the estimated self-motion.

The use of multiple sensory channels may also be advisable if the dynamic range of any one channel is smaller than required for locomotor control. In Crustacea, Molluses, and Vertebrates, including man, eye movements are controlled bimodally. In many instances the mechanosensory mechanisms tend to be fast but not very accurate, whereas visual mechanisms tend to be slower but more precise (Budelmann 1990, Dichgans 1983, Dieringer 1986, Sandeman 1983). Does this notion also apply for *Calliphora*?

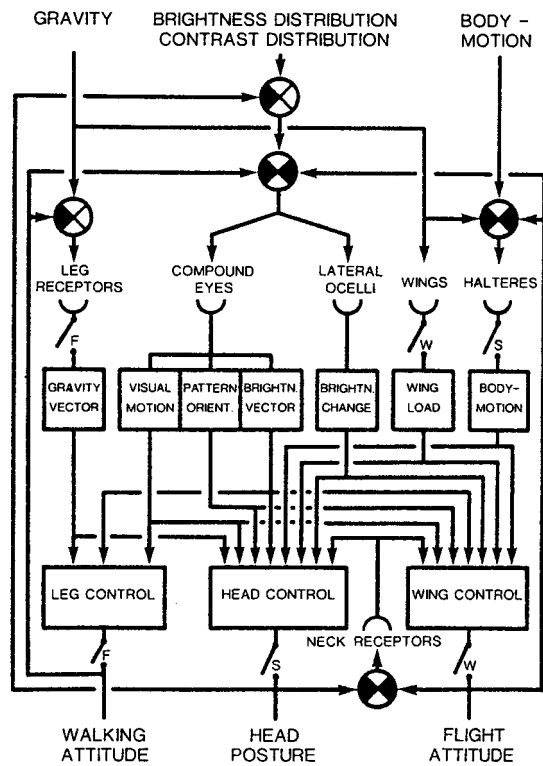


Figure 4: Signal flow diagram of roll control in *Calliphora*. It illustrates the effective cues, the sense organs involved, the signal processing stages that can be logically separated, the distribution of signals on motor control networks, and the physical reduction of error signals by motor actions (black sectors of summation points). Switches are opened by different locomotor states (F = flying, W = walking, S = standing) to ensure appropriate signal routing.

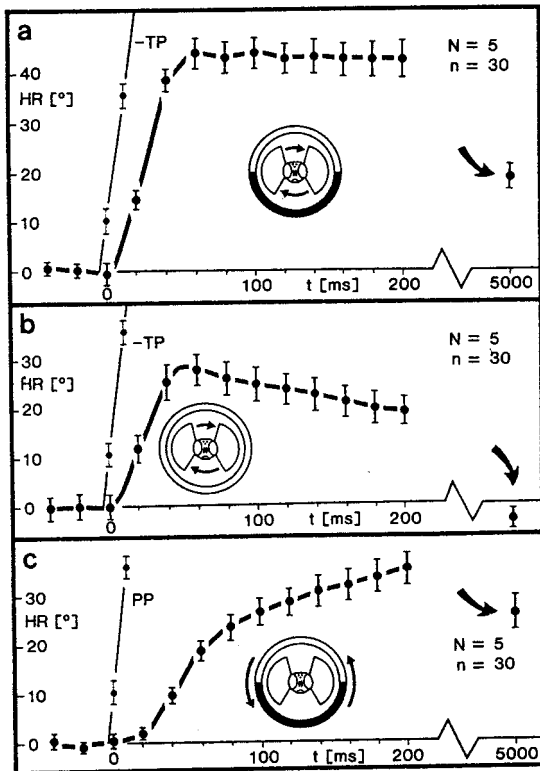


Figure 5:

Time course of head turns in response to step stimuli (90° , $2000^\circ/\text{s}$). (a) A fly, tilted by -90° within the sky-and-ground pattern generates, after a short delay (ca. 10 ms) a fast head roll ($1200^\circ/\text{s}$) which is maintained for many seconds (see arrow and time scale). (b) Tilting the fly in visually homogeneous surrounding: elicits, after a short delay (ca. 10 ms), a fairly fast head roll ($700^\circ/\text{s}$) that disappears within 5 seconds (arrow). (c) Stepwise displacement of the pattern elicits a head roll after a much longer delay (ca. 30 ms) which rises slowly ($450^\circ/\text{s}$) to a maintained level. Apparently, the combination of visual and mechanosensory mechanisms (b, c) yields the superior performance shown in (a).

To test this hypothesis the time course of head turns was recorded in response to angular step displacements (Fig 5a-c; 90° at $2000^\circ/\text{s}$; note that the sign of stimuli is chosen to facilitate the comparison of response curves). If the fly is rolled in optically structured surroundings (Fig 5a) it turns its head after a short latency (10 ms) with high speed ($1200^\circ/\text{s}$) against the imposed misalignment and maintains, after some adaptation, a compensatory posture for a long time (Fig 5a; arrow). If the sky-and-ground pattern is removed and the fly is turned through 90° (fig 5b), it responds equally after a short delay (ca. 12ms) and with fairly high speed ($700^\circ/\text{s}$) but the response fades completely within 5 seconds (Fig 5b, arrow). This proves that the mechanosensory channel is fast and that the steady state response is caused visually. If, conversely, the fly is held stationary and the sky-and-ground pattern is rolled through 90° (fig 5c), the fly starts to turn its head only after a much longer delay (30 ms) and at a lower speed ($450^\circ/\text{s}$). The corrective head turn is, however, maintained for a long time (Fig 5c, arrow). The combination of the mechanosensory response component (Fig 5b) and the visual component (Fig 5c) provides the fly with the quick, fast, and maintained head realignment shown in Fig 5a. For this „dynamic complementation” of responses it is necessary, and has been demonstrated, that the component responses can be elicited independently. As a consequence of this, *Calliphora* can stabilize its head effectively at all speeds that a fly may encounter in real life.

Conclusions

Flies have a sophisticated and powerful gaze control system. It allows them to stabilize, during walking and flight, the orientation of their eyes relative to the surroundings. Hence they can see better during locomotion than their visual system would allow if the eyes were fixed to the trunk. This is especially true while flies proceed along their aerobatic flight trajectories.

The striking similarities of functional organization in gaze control systems of different animals and the accessibility of neural constituents in the fly makes this system particularly attractive for physiological studies.

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